ANTAGONISM—THE BACKGROUND TO SOIL FUNGI

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As ecology is the central and centralizing discipline of biological science, it is fortunate that current works on general ecology show a considerable amount of agreement on terminology and understanding of the concepts used. Clarke (1954) and Odum (1954) discuss the possible forms of interaction between pairs of species, and both subscribe to the system of description evolved by Haskell (1949) in the field of social science, and later applied more widely by Burkholder (1952). *Antagonism* is one main subdivision (the other being *symbiosis*) and includes all those associations in which at least one of the interacting species is harmed. The mechanisms of antagonism are three; namely, *antibiosis* in which species *A* produces a chemical substance that is inimical to species *B* without species *A* deriving any direct benefit, *exploitation* in which species *A* inflicts harm by the direct use of species *B* for its own benefit, and *competition* which is found in the indirect rivalry of two species for some feature of the environment that is in short supply. There are obstacles to the complete acceptance of these definitions; an important one is that 'competition' has, in addition to the strict meaning given above, a wider meaning equating it with antagonism. This Darwinian usage is difficult to avoid in certain contexts, e.g. in the verbal form as when 'two species compete for a substratum'. Similarly the broad concept is implied in the phrase 'competitive saprophytic ability', the precise meaning of which has been amply set forth by its author (Garrett, 1956). In unavoidable cases such as these the context usually makes it clear that 'antagonism' is referred to, while for most purposes the more strict definitions are gaining acceptance.

Despite the lack of terminological standardization in the earlier literature, it is apparent that all three mechanisms have been cited by various authorities to account for the antagonisms among soil fungi, and probably all are responsible in some degree. Exploitation, as represented by the parasitism of fungal hyphae by others, has undoubtedly been demonstrated, yet most emphasis has been laid on competition and antibiosis. There has been much controversy over the relative importance of these two processes. This controversy has its origin, it would seem, not in the fact that the two processes are mutually exclusive but in that workers have applied Occam's razor, and looked for a single general mechanism to explain the universal phenomenon of fungal inhibition in soil. Since this fungistasis is such a universal phenomenon, associated, not with specific factors but generally with the distribution and intensity of fungal activity (Dobbs & Hinson, 1953; Jackson, 1958), this is a more logical procedure than to explain some examples by antibiosis and others by competition. Some arguments in favour of antibiosis rather than competition have been put forward by Park (1956*b*); these will be extended and stated in more detail here.

It is common experience that fungi, although heterotrophic, can grow in nutrient solutions containing only low concentrations of nutrients. Examples of such growth are found in the continuous growth that occurs in a medium of distilled water and agar, in the growth of fungal colonies in laboratory mineral reagents, and in the growth over clean glass surfaces (Smith, 1946). In the light of these facts, when considering the probability of competition for nutrients as a mechanism in the production of the fungistatic property of soils, the following comment by Odum (1954) seems apt:

> In a study of a particular situation the ecologist can usually discover the probable weak links and focus his attention, initially at least, on those environmental conditions most likely to be critical or 'limiting'. If an organism has a wide range of tolerance for a factor which is relatively constant and in moderate quantity in the environment, that factor is not likely to be limiting.

In this connexion it seems to have slipped out of focus that fungi have an extraordinarily wide range of tolerance for low levels of nutrients. Moreover, it is easily demonstrated (Park, 1956*b*) that a soil solution does contain sufficient nutrients to support fungal growth. There is of course the possibility that low-nutrient status might emphasize the susceptibility of fungi to retarding factors other than competition, as demonstrated by Brown (1922); this could make low nutrients seem more directly responsible than is actually the case. The theory of competition for nutrients, has been supported, among others, by Thornton & Skinner (1953), who have accompanied their views with the statement that 'workers have too often tended to ignore this factor of competition for nutrients, and to attribute antagonism wholly to the action of antibiotic secretions. More experiments are needed that aim at distinguishing these two factors'. I would point out that in respect of this general antagonism in soil such experiments are unnecessary, since it is known that the fungistatic factor maintains fungal structures in an inactive condition. It is difficult to imagine that inactive propagules should compete for nutrients, or should be inhibited by lack of nutrients when most are able to resume activity without any external source of nutrients. For these reasons, therefore, and for others given later, competition for nutrients does not satisfactorily account for the widespread type of antagonism that occurs between fungi in soil.

Competition for space has been named as a mechanism operative in fungal antagonism in soil. In an analysis of the validity of any concept, it is necessary to take the words at their true meaning. Competition for space, then, implies that organisms compete primarily for physical dimensions that, in an otherwise more suitable environment, exist in amounts insufficient to accommodate the bodies of the organisms together. In motile organisms of a high degree of organization, the space concept may be less simple, as may be illustrated by reference to foraging animals or to animals with territorial breeding requirements, but in non-motile individuals space properly refers to those dimensions necessary to house the body of the organism. Among higher plants one may find examples of competition for space in this strict sense—in a radish plot where swelling tap-roots may lift plants completely out of the ground, or among the rhizomes of the floating mat vegetation at the borders of lakes, where the aqueous medium provides ample nutrients and removes metabolic products. The condition of a substratum being so intensively colonized by fungal mycelium as physically not to allow of penetration by another hypha must be comparatively rare. Examples may be found in the mummification of a parasitized substratum by such fungi as *Sclerotinia fructigena* and *Cordyceps militaris*. Elsewhere among microbes competition for space may be found among the organisms colonizing sewage filters in a continuous flow of nutrient medium which also removes staling products, although even here it is difficult to visualize a potential colonizer of such a closed community 'competing' for space without employing some other means of antagonism to displace or incapacitate its predecessor on the site.

A microscopic examination of soil or of decomposing organic materials in soil shows that fungal structures are normally not sufficiently numerous to be able physically to prevent further fungal development there. Competition for space, in fact, is not conceivable as a mechanism underlying the general antagonism in soil. Any space unoccupied by structures, and which is unsuitable for colonization, does not itself act as a factor in antagonism, but as a medium through or in which some other mechanism operates. It may be that with more space available further development would occur, initially at least, but the additional space would be acting by attenuating the other inhibiting factor by, e.g., absorbing or diluting toxins. Thus the problem is one of *space-plus*, or *Lebensraum*, rather than of space in the strict sense. To argue that the term 'competition for space' does not imply space in a strict sense is merely to replace one indefinite concept by another, and defers the consideration of the real problem a stage further.

It is my aim here to show that antibiosis more easily accounts for the general antagonism in soil. Unfortunately the concept of antibiosis has become associated almost inseparably with the study of specific antibiotics. From Waksman's (1945) discussion of the term 'antibiotic', current ideas have narrowed and become more and more confined to considerations of potent, complex, and usually chemotherapeutic substances. Almost all recent discussions of the significance of antibiotics in Nature are limited, explicitly or implicitly, to well-characterized, specific compounds, while simpler and more general compounds, such as carbon dioxide and lactic acid which the original definition includes, are omitted or excluded. Problems relating to the production and activity in soil of the specific type of antibiotic have received much attention. This subject has recently been reviewed in detail by Brian (1957), and lists of references on the items in the following sentences may be found in that article. Many workers have shown that such specific compounds may be produced in detectable amounts in soil, which in most cases was sterilized or greatly amended with energy materials. Jefferys (1952) has shown clearly that some of these antibiotics are stable under certain conditions on addition to the soil, and may exert an effect there. On the other hand, much work has gone to show that a number of specific antibiotics are degraded biologically in soil, or are there inactivated by adsorption on to colloidal materials. Such data, which suggest that specific antibiotic substances are not produced or are not active in soil, have been used to support arguments to the effect that the action of antibiotics in soil is, if operative at all, small and local. These arguments have little bearing on the general significance of *antibiosis* in soil, which is more probably mediated by simple toxic compounds than by specific antibiotics. In the same way positive proof of the local action of specific antibiotics, although of interest in connexion with the particular situation under investigation, and of probable significance there, may have less relevance to the general phenomenon of antibiosis in soils in which some mechanism of widespread occurrence and general validity must be operative.

In this respect much early work in this field, performed before the acceptance of the 'antibiotic' conception, is relevant, and shows that non-specific substances may account for the soil antagonism and that this phenomenon may be explained without reference to highly complex antibiotics. Schreiner & Shorey (1910) and Waksman (1936) give lists of chemical compounds that may be found in soil; many of these compounds are toxic to fungi. Greig-Smith (1912), Neilson-Jones (1941), Waksman & Woodruff (1942), and Newman & Norman (1943) are among those who have demonstrated the presence of fungi-toxic substances at inhibitory levels in soils. Further, it is known that common compounds of relatively simple nature may occur in soils at levels high enough to exert toxic effects, e.g. nitrites (Waksman, 1931), cyanides (Timonin, 1941), and carbon dioxide (Garrett, 1936). In using examples from the familiar literature to show that substances having an antibiotic effect do, in fact, occur in normal soils in quantities sufficient to inhibit fungal development, it is not my claim to introduce anything new, merely to point out the significance of what has been overlooked both by those authors who argue against antagonism by antibiosis and by those who propose a general antibiosis mediated specifically by antibiotics of the restricted type. 'Espinasse (1944) has criticized the use of the term 'antibiotic' for what is an aspect of a broader phenomenon. The concept of 'external metabolites', suggested by Lucas (1947), develops this idea further, and might serve as a means of avoiding some of the confusion surrounding the discussion of antibiotic substances.

The normal inactivity of fungi in soils is most easily overcome by adding amendments of various sorts to soil. Evidence of this type has usually been taken to support theories of competition rather than antibiosis, more especially since the amendments have usually contained food materials. In cases such as these, however, it has not been thought necessary to show that that amendment was effective through a direct amelioration of nutrient deficiency; this has usually been assumed. Even if it could be shown that such a stimulation were due directly to a higher nutrient status, the antibiosis hypothesis might still be applicable on the basis of the maxim already recalled, that inhibitory substances have their greatest effect when the energy of growth is small, and that an increase in the amounts of available nutrients may enable an organism to overcome a positive inhibition (Brown, 1922). But the nutrient effect is not the most reasonable explanation of the action of amendments. It has repeatedly been found that insoluble amendments to soil have a greater stimulatory action on the inhibited soil microbia than do soluble amendments (Rayner, 1939; Katznelson & Chase, 1944; Bingeman, Varner & Martin, 1953; Park, 1955; Chinn & Ledingham, 1957). Park (1956*a*) has shown, in addition, that non-nutrient but insoluble amendments may stimulate activity in similar toxic habitats. These facts invalidate the hypothesis of competition for nutrients as a cause of the inhibition. There are two other possible interpretations. The first, that the insoluble additions provide space and relieve competition for this factor need not further be considered; the second, that the amendment provides a fresh physical substratum in which there is no accumulated level of antibiotic substances has been preferred (Park, 1956*a*, *b*).

A useful analogy may be made between the condition of fungi in soil and in old cultures on agar. In pure culture a fungus may fill the Petri dish before cessation of growth, but in this condition spaces in the agar remain unoccupied by hyphae. The fungus is inhibited by the accumulation of autotoxic metabolic by-products or staling substances, and not by the depletion of nutrients (Boyle, 1924; Pratt, 1924; Waksman & Foster, 1937) or of space. Tribe (1957) has given an ingenious demonstration of how the same process can occur in soil: here cellulose film buried in soil eventually became unsuitable for further growth of cellulose-decomposing fungi, although some cellulose remained. The staling of fungal cultures is by definition an example of antibiosis, and has, in fact, been considered by Waksman (1937) as *iso-antagonism* comparable with the *hetero-antagonism* found in soils. In a staled pure culture of a fungus, as in soils, a block of non-nutrient agar gel added to the surface stimulates the inhibited fungus to activity, and for the same reasons. If, then, soil is regarded in the light of a fungal culture medium in this way, normal field soil is a medium that has been inoculated with a complex mixed culture of fungi and other organisms, and incubated for long periods under varying cultural conditions. Obviously, in such a medium metabolic products of diverse types have accumulated, and have resulted in an intense example of the sort of inhibition that occurs even in a pure fungal culture in which the fungus is not a recognized antibiotic producer. On this basis the fungal population of any settled soil is normally in an advanced stage of what has been described as 'Altkultur', and shows the inhibited, abnormal, and disintegrating spores and hyphae characteristic of that state (Appel & Wollenweber, 1910). This condition has also been described from experimental cultures of individual fungi in sterilized soil. So-called 'sick soils' that are characterized by an unusually high level of toxins (Waksman, 1937) may be regarded as extreme examples of staled cultures.

In short, then, theories of competition for nutrients or space fail adequately to account for the phenomenon of antagonism in soils in a general sense. A basis for an explanation of the phenomenon lies in facts familiar to all microbiologists, so that it is superfluous to postulate in all cases of antagonism the action of specific antibiotic substances, the antibiosis being brought about by either a general toxic substance or by a complex of toxins produced by many organisms.

Implicit in the foregoing arguments are certain views on the significance of antibiotic production. Before expanding these, I should like to point out that discussions on this topic usually consider two separate aspects of significance; firstly, the immediate importance of the production to the species which produces the antibiotic, and secondly, the significance of the production in the biology of the habitat. Although separate, these two facts are conveniently discussed together. The idea of an antibiotic being of direct value to the organism producing it has been criticized on the grounds that it implies a purposiveness on the part of that organism; Brian (1957) has adequately disposed of this argument, which seems to be based on the misconception that to ascribe a function to a process in an organism is to accept that the organism evolved the process with a foreknowledge of the function that it would perform. Garrett (1956) has dealt with, and disposed of, three other main arguments against the antibiotic value of antibiotics to the organisms that produce them. Other arguments may be raised. An antibiotic is a toxic compound, and there are indications that organisms producing such compounds are not immune to their action, but merely possess a high degree of tolerance to high concentrations of them. It is, therefore, probable that the external secretion of compounds of this sort is essentially an elimination of autotoxic metabolites. The primary function, and hence value to the organism, of such 'secretion', then, may be the elimination of toxicity. Antibiotic production, on this view, has its individual significance for the producer-organism in excretion, and is independent of any possible action on other organisms.

Other arguments consider both types of significance together. Brian (1957) argues in the following way in support of the advantage conferred on organisms by the capacity to produce an antibiotic.

> Organisms sensitive to antibiotics are at a disadvantage where they have to compete with antibiotic producers for limited substrates. If that conception is valid, I think it is reasonable to conclude that what is a disadvantage for one group of organisms may be an advantage for others. If that is so, the capacity to produce antibiotics must be expected to increase the likelihood of survival of a saprophytic species.

This statement expresses one of the main arguments of the supporters of the theory that antibiotics have an immediate beneficial effect on the organism which produces them, and is therefore worth examining in some detail. The major error in the argument is that the two types of organism that are compared—namely, those 'organisms sensitive to antibiotics' and the 'antibiotic producers'—are assumed to be two different and separate categories; in fact, this need not be so. Butler (1953) and Park (1956*b*) are among those who have shown that organisms not recognized as producers of antibiotics may have a higher tolerance of antibiosis than some organisms that exhibit antibiotic activity. Some misconceptions in this respect have arisen as a result of thinking in terms of artificially mixed cultures of only two organisms, and with those growing towards each other as colonies. This condition is remote from that usually occurring in Nature, where the colony as such may not exist, and where many more than two organisms are in the same sphere of influence and are probably simultaneously active on those occasions when conditions favour activity. If, in such a situation, fungus *A* produces an antibiotic at a concentration to which some associated organisms are sensitive, and to which others, including *A*, are tolerant, then the degree of advantage gained by *A* will not be simply determined, but will depend on many factors, among which the following are particularly relevant: (i) the relative numbers of the sensitive and the tolerant organisms; (ii) the distribution within these two categories of organisms able to inhibit *A* itself; (iii) the proportion of sensitive organisms that would, in the absence of the antibiotic produced by *A*, be able to inhibit the antagonists of *A*. Two hypothetical situations will illustrate this more clearly; in both of these, four organisms occur together, and have equal demands on the habitat.

1st situation: A grows and produces an antibiotic that inhibits *B*, *C*, and *D*. Thus *A* has the substratum to itself—an obvious advantage.

2nd situation: A inhibits *B*, but *C* and *D* are tolerant of *A*'s antibiotic. *B*, when active, inhibits *C* and *D*, but has no adverse effect on *A*. In the presence of *A*, of course, *B* neither grows nor produces its antibiotic, and so *C* and *D* grow. *A*, therefore, shares the substratum with two organisms, whereas were it not to produce the antibiotic it would share it with only one organism.

The first type of situation is the one usually assumed by the protagonists of the hypothesis of an individual beneficial effect of antibiotic production. The second situation illustrates a perfectly possible type of set-up (cf. Lochhead & Landerkin, 1949) in which antibiotic production may be a disadvantage. Although this situation is hypothetical and a simplification, it is a much greater simplification to assume that because an organism produces an antibiotic it automatically has an advantage.

An extension of the above reasoning shows that an organism that has a wide tolerance of antibiotics, irrespective of any ability to produce antibiotics, has a high chance of success in mixed cultures. The fact that tolerance to antibiotics is an important character in ecological success is recognized by most authorities, and has been cited as such in a number of review papers (e.g. Garrett, 1950; Hawker, 1957), including the one containing the statement quoted (Brian, 1957). Garrett (1956), in his discussion of competitive saprophytic ability, lists this character as one of the four likely to favour a high competitive saprophytic ability. The other three are high growth rate and rapid germinability of spores, good enzyme-producing equipment, and the production of antibiotic toxins. The argument advanced in this present essay would, in reference to any toxic situation, relegate these three characters to a role subsidiary in importance to tolerance to antibiosis. An organism sensitive to the antagonism to which it is exposed might possess such characters but be unable to express them. A clear example has been given by Park (1956*b*) of an organism (*Trichothecium roseum*) having a high antibiotic activity yet being unsuccessful in mixed cultures due to its low tolerance to antagonism. So that although the capacity to produce antibiotics is a character conducing to fitness (Brian, 1957), it is a secondary character, tolerance to the antagonism existing in soil being the primary requirement of any soil fungus that inhabits situations in which the general fungistasis exists.

There are some conditions in which an organism producing an antibiotic has a clear-cut advantage, irrespective of its sensitivity to antibiosis from other organisms. These are those conditions of Nature which compare closely with laboratory conditions of culture. One of these is the situation of a pioneer or primary colonizer of a substratum which can grow and produce its antibiotic freely and without interference. Here, an organism that is sensitive to antibiosis and unable to colonize any substratum that is already occupied by other organisms may, when established in a newly available substratum, continue to be active and survive, and may even exclude those organisms to which it is, in other circumstances, sensitive (e.g. Simmonds, 1947; Wright, 1956; Tribe, 1957; Barton, 1960). In some of these cases it is noticeable, however, that the initial colonizers able to exclude other organisms are not recognized producers of antibiotics. It is in a situation of this type, in which the organisms are, in part, dependent upon a sustained high inoculum potential, that antibiotic activity may have considerable individual significance for the organism possessing it. Furthermore, under the conditions of this sort the other characters listed by Garrett (1956) as important in respect of competitive saprophytic ability (e.g. high growth rate, etc.) become primary and tolerance to antibiosis secondary. This is because the organism exists in a non-toxic environment. Despite the tendency, through the high inoculum potential, of such a system to be self-perpetuating, these organisms do eventually bring about a change in the substratum both through nutrient loss and through staling, so that it eventually becomes unsuitable for their continued development there. It is one of the causes of succession, therefore, that an organism may be more sensitive to its own antibiotic products than are other organisms that succeed it in time.

Clements (1916, 1935) has considered some topics that are appropriate to this discussion of background antagonism; in particular, his definitions of action, co-action and re-action are of direct relevance. *Action* is the effect of the abiotic habitat on the organism; *co-action* is the direct effect of one organism on another; *re-action* is the effect of the organism on the abiotic environment. The idea of antibiotic production directly and solely favouring those organisms that produce them seems to be based on the conception of antibiosis as a form of co-action. Co-action may occur, but is special and restricted. The arguments that have been put forward in this essay favour the view that antibiosis is an ecologically significant factor mainly in the form of a re-action that is followed later by action. In other words, the organisms in a habitat produce substances that are added to the abiotic environment, from which they subsequently affect the other organisms under the influence of that modified environment. Soil antagonism is in this sense a non-specific background effect, cumulative and common in its production by all the organisms present, and acting on all those organisms.

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